

WERE ALL PTEROSAURS OVIPAROUS?

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ABSTRACT Much progress has been made recently in understanding pterosaurs, Mesozoic flying reptiles, and some basic aspects of their palaeobiology, phylogenetic relationships and evolutionary history are now generally agreed upon. Studies of pterosaur reproductive biology have been kick-started by the discovery of three eggs, with embryos, each apparently representing a different species of pterosaur. Two finds in the Lower Cretaceous Yixian Formation of China belong to pterodactyls and in one case can be confidently assigned to the Ornithocheiridae on the basis of distinctive proportions of the limb bones (such as the relatively short third metatarsal and the relatively long fore-limb), and morphological features including the warped deltopectoral crest of the humerus. A third embryo from the Lower Cretaceous of Loma del *Pterodaustro* in Argentina compares extremely closely to hatchlings and older individuals of *Pterodaustro guinazui*, the only pterosaur known from this site, and undoubtedly belongs to this species. Several lines of evidence support the idea that oviparity was universal in pterosaurs: (1) oviparity in ctenochasmatids and ornithocheirids suggests, as a minimum inference, that all pterodactyls, at least, were oviparous; (2) oviparity is widespread in diapsids and, irrespective of the exact location of Pterosauria within this clade (currently much debated), oviparity in pterosaur ancestors is much more likely than viviparity, especially if pterosaurs prove to be ornithomimids; (3) the complete absence of any evidence, so far, for viviparity in pterosaurs. The likelihood that they had a poorly calcified, or possibly even non-calcified pliable or parchment-shelled egg is probably the main reason why pterosaur eggs are so rare compared to those of other groups such as dinosaurs and birds, which have well calcified hard shells.

INTRODUCTION

Establishing the biological attributes of wholly extinct organisms that have no close living relatives and with uncertain relationships to other groups is both one of the key tasks and greatest chal-

From: Lü, J. C., Kobayashi, Y., Huang, D. & Lee, Y.-N. (eds). 2006. *Papers from the 2005 Heyuan International Dinosaur Symposium*. Geological Publishing House, Beijing. 141 ~ 167.



lenges for palaeontology. Several classic examples of such problem taxa are to be found among the vertebrates. Ichthyosaurs, a clade of fully marine Mesozoic diapsids, whose origins and relationships to other diapsids, locomotory ability and general mode of life are still much debated, provide an excellent example (McGowan and Motani, 2003). However, the degree of intractability posed by these rather dolphin-like swimmers, or other problem groups such as the plesiosaurs, is easily surpassed by one particular lineage of Mesozoic tetrapods that has proven especially difficult to understand: pterosaurs.

Pterosaurs, a highly unusual, diverse and important clade of Mesozoic flying reptiles, were first discovered and described in the late 1700's on the basis of a superbly preserved complete skeleton from the Upper Jurassic Solnhofen Limestones of southern Germany (Wellnhofer, 1984). This fossil, now the holotype of *Pterodactylus antiquus*, provoked a great deal of controversy and although recognized by some, such as Cuvier, as a flying reptile, was also variously interpreted as a sea creature and a marsupial bat (Wellnhofer, 1984, 1991). It was not until the publication of the first substantial review of these animals, in von Meyer's 'Zur Fauna der Vorwelt' (1859), that it became widely established that pterosaurs were reptiles. Despite this progress, many aspects of pterosaur biology including the nature of their flight ability, how they moved on the ground, their physiology, their interrelationships and their evolutionary history, remained poorly understood and frequently triggered fierce debates. Different opinions concerning pterosaurs' likely body temperature, and its implications for their physiology, for example, led to a sharp exchange of views between Richard Owen (1870) and Harry Seeley (1870a), a row that was repeated 50 years later, with even greater animosity, by Gustav Arthaber (1922) and Baron Franz von Nopcsa (1924).

In the last two decades considerable progress has been made with regard to understanding many (although by no means all) problematic aspects of these animals. This has led to a general understanding of pterosaur palaeobiology that is both reasonably consistent and coherent, and has also helped to explain several major features of pterosaur evolution such as the remarkable morphological and ecological conservatism of basal clades and the apparent restriction of pterosaur tracks to the Late Jurassic and Cretaceous (Unwin, 1999, 2005; Unwin and Henderson, 2002; Naish and Martill, 2003).

Three factors underlie this progress. First, and without doubt the most important, is the discovery, in the last few decades, of a plethora of new fossil remains (Wellnhofer, 1991; Buffetaut and Mazin, 2003; Unwin, 2005). Among these are many important finds including almost complete uncrushed skeletons from the Lower Cretaceous Santana Formation of Brazil (Kellner and Tomida, 2000) and some spectacular examples of soft tissue preservation, notably from the Upper Jurassic Solnhofen Limestones of Germany (Wellnhofer, 1987, 1991; Padian and Rayner, 1992; Frey *et al.*, 2003), but also from the Upper Jurassic Karatau Mountains of Kazakhstan (Sharov, 1971; Unwin and Bakhurina, 1994), the Santana Formation (Martill and Unwin, 1989) and underlying Crato Formation (Campos and Kellner, 1997; Frey *et al.*, 2003) of Brazil and the Jehol Group of north-east China (Lü, 2002; Wang *et al.*, 2002). Certainly of no lesser importance is



the burgeoning pterosaur track record (Unwin, 1997), which has finally resolved the long standing debate over the terrestrial ability of pterosaurs, showing them to have been exclusively quadrupedal and plantigrade when grounded (Lockley *et al.*, 1995; Mazin *et al.*, 1995; Fig. 1A), a conclusion that is consistent with studies of osteology and arthrology (Wellnhofer, 1988; Unwin, 1999) and computer models (e.g. Henderson and Unwin, 2001).

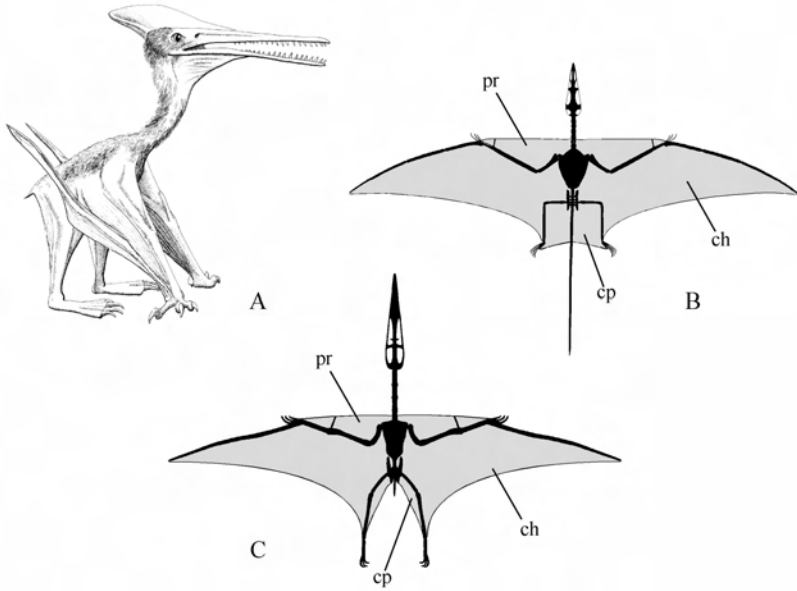


Fig. 1 Current ideas regarding pterosaur anatomy.

A, *Pterodactylus*, wingspan about 0.5 m, standing in a quadrupedal plantigrade posture and restored with a cranial crest, pelage, a cheiropatagium attached to the fore and hind limbs, a cruropatagium and webbed feet; **B**, restoration of a 'rhamphorhynchoid' pterosaur (*Sordes*, wingspan about 0.6 m) in dorsal view, **C**, restoration of a pterodactyloid pterosaur (*Pterodactylus*) in dorsal view (all redrawn from Unwin, 2005).

The second factor relates to new methodologies, most notably cladistics, and techniques, such as Computer Automated Tomographic scanning, both of which have yielded critical new insights. The former (see, for example, Bennett, 1989, 1994; Unwin, 1995, 2003a, 2004; Unwin and Lü, 1997; Kellner, 2003) have helped establish a radically new view of pterosaur interrelationships, showing that 'rhamphorhynchoids' are paraphyletic and that pterodactyloids can be resolved into four major clades. The latter has revealed fine details of neural anatomy that can be used to infer pterosaur head posture during locomotion and hint at the exciting possibility that pterosaurs had clever wings, with flight membranes whose shape and tension were monitored and controlled by the brain (Witmer *et al.*, 2003; Unwin, 2003b). In addition, implementation of older techniques such as ultra-violet light photography has yielded spectacular new information concerning the shape and internal structure of the wing membrane and other soft tissue structures such as foot webs and cranial crests (Frey and Tischlinger, 2000, 2003; Tischlinger and Frey, 2001, 2002; Frey *et al.*, 2003; Tischlinger, 2003).



The third factor concerns what might be termed the modern renaissance in pterosaur studies. In the 1970's few palaeontologists studied pterosaurs and only two or three, most notably Peter Wellnhofer, focused particular attention on the group. From the early 1980's onwards there has been a marked increase in activity. In the last ten years, for example, the rate of publication has reached 10 – 15 papers per year, compared with 2 – 5 in the 1970's. Moreover, at least 40 different researchers have contributed to these papers and at least 10 of these regularly publish on pterosaurs. At the present time the intensity of this work shows no sign of slowing; more than 10 papers and a book devoted to pterosaurs were published in 2005 and the surge of discoveries in north-east China (e. g. Wang *et al.*, 2005) is likely to lead to an even greater increase in activity.

The main result of this rapidly growing fossil record, application of new techniques and renewed interest in the group has been the emergence of a well integrated and widely accepted set of ideas concerning pterosaur anatomy, locomotion, physiology, relationships and evolutionary history. The general skeletal anatomy of pterosaurs is now fairly well understood, although some regions such as the nature and relationships of the ossifications contributing to the base of the brain-case have yet to be fully elucidated. Thanks to fossil remains from at least seven different localities, the soft tissue anatomy of pterosaurs is perhaps better understood than for almost any other Mesozoic group (Martill and Unwin, 2003; Unwin and Martill, 2003). The spectacular nature of pterosaurs' cranial crests, some of which are continued in soft tissue, has been well documented (Campos and Kellner, 1997; Martill and Frey, 1998; Bennett, 2002; Frey *et al.*, 2003) and the general external morphology of the brain is now quite well understood (Witmer *et al.*, 2003). Fossilised soft tissue evidence of bristles fringing the jaws, throat sacs, what may be sections of the gut, tail flaps and foot webs have also been found (reviewed in Unwin, 2005). Skin is preserved in several pterosaurs and in some cases bears evidence of fine, short 'hairs' (see e. g. Wellnhofer, 1991; Frey and Martill, 1998; Wang *et al.*, 2002). Fig. 1A shows a *Pterodactylus* reconstructed on the basis of all currently available evidence regarding pterosaur skeletal and soft tissue anatomy combined with the results of recent studies of their stance and gait on the ground.

Critically, some of the new finds of fossilised remains, or impressions, of the wing membranes has enabled us to establish the shape and extent of the wings in several groups. It appears that basal clades such as anurognathids (Wang *et al.*, 2002) and scaphognathines (Unwin and Bakhurina, 1994) had extensive flight surfaces that extended in front of the fore-limb, between the fore and hind limb, and even between the hind limbs (Fig. 1B). Pterodactyloids had a similar arrangement, but with one critical exception, the membrane between the hind limbs was separated into two along the mid-line (Fig. 1C), effectively breaking the linkage between the limbs on the left and right side of the body. This is likely to have been of some significance for flight, but was even more critical on the ground, where it seems to have endowed pterodactyloids with a much more effective terrestrial ability than that of basal groups (Unwin, 2005).

The internal anatomy of the wing membranes has recently been shown to be highly complex (Martill and Unwin, 1989; Frey *et al.*, 2003; Lü *et al.*, 2005). In addition to aktinofibrillae there is evidence of a vascular layer, muscles fibres and blood vessels. This indicates that, in con-



trast to the ‘dead’ wings of birds, pterosaurs had ‘live’ wings, like bats. Moreover, it seems likely that the structure of the membranes enabled pterosaurs to exhibit considerable control over the shape of the various flight surfaces (Unwin, 2003b, 2005; Witmer *et al.*, 2003). This hints at a complex and sophisticated flight ability, which matches the results of studies of skeletal anatomy (e.g. Wellnhofer, 1975, 1978; Padian, 1983; Bennett, 2001) and recent analyses of the aerodynamics of pterosaurs such as the large Early Cretaceous ornithocheirid *Coloborhynchus* (Wilkinson, 2003; Wilkinson *et al.*, 2005).

At present pterosaurs are represented by just over 100 species (compared to almost 9500 extant and over 2000 extinct species of birds) with an adult size that ranges from less than half a metre to over ten metres in wingspan. The earliest records are from the Upper Triassic (Norian) and fossil remains have been found in almost all intervening stages through to the end of the Cretaceous. The fossil record is highly uneven, however, and much of what is known about the group stems from a handful of Lagerstätten largely concentrated in what was Laurasia and often separated by long temporal gaps in which finds are, at best, scanty. Problems with the fossil record notwithstanding, by combining available data on the stratigraphic distribution of fossils with recent phylogenetic analyses of pterosaur interrelationships (Bennett, 1989, 1994; Unwin, 1995, 2002, 2003a, 2004; Unwin and Lü, 1997; Kellner, 1996, 2003, 2004; Maisch *et al.*, 2004) it has been possible to develop a relatively detailed picture of pterosaur evolution (e.g. Unwin, 2005; Fig. 2).

Following a basal radiation in the Late Triassic, several early clades (e.g. dimorphodontids, campylognathoidids) seem to have become extinct in the Early Jurassic and were replaced by more derived long-tailed forms (scaphognathines, rhamphorhynchines). After dominating much of the rest of the Jurassic these lineages seem to have died out at the end of the Jurassic or possibly in the Early Cretaceous.

Basal clades seem to have been quite conservative, at least in terms of their postcranial skeletal morphology, whereas the pterodactyloids, which underwent an evolutionary radiation in the early Late Jurassic, were much more diverse. The key to pterodactyloid’s success may be related to their improved terrestrial ability, compared to ‘rhamphorhynchoids’, which allowed them to radiate into many new ecological niches such as filter-feeding, where competency on the ground was important.

By the Early Cretaceous the pterodactyloid radiation was firmly underway. Pterosaurs seem to have achieved their greatest diversity during this time since all four major pterodactyloid clades, together with a late surviving basal clade (Anurognathidae) are represented in this interval. Several lineages (ctenochasmatooids and dsungaripteroids) seem to have become extinct by the end of the Early Cretaceous, and all toothed forms seem to have disappeared by the early Late Cretaceous, leaving just two clades of toothless forms. The first of these, the pteranodontians, seem to have survived to the end of the Cretaceous, but are rare after the early Campanian. By contrast, the azhdarchooids almost completely dominate the Campanian and Maastrichtian pterosaur record, some of them achieving large and even giant size.

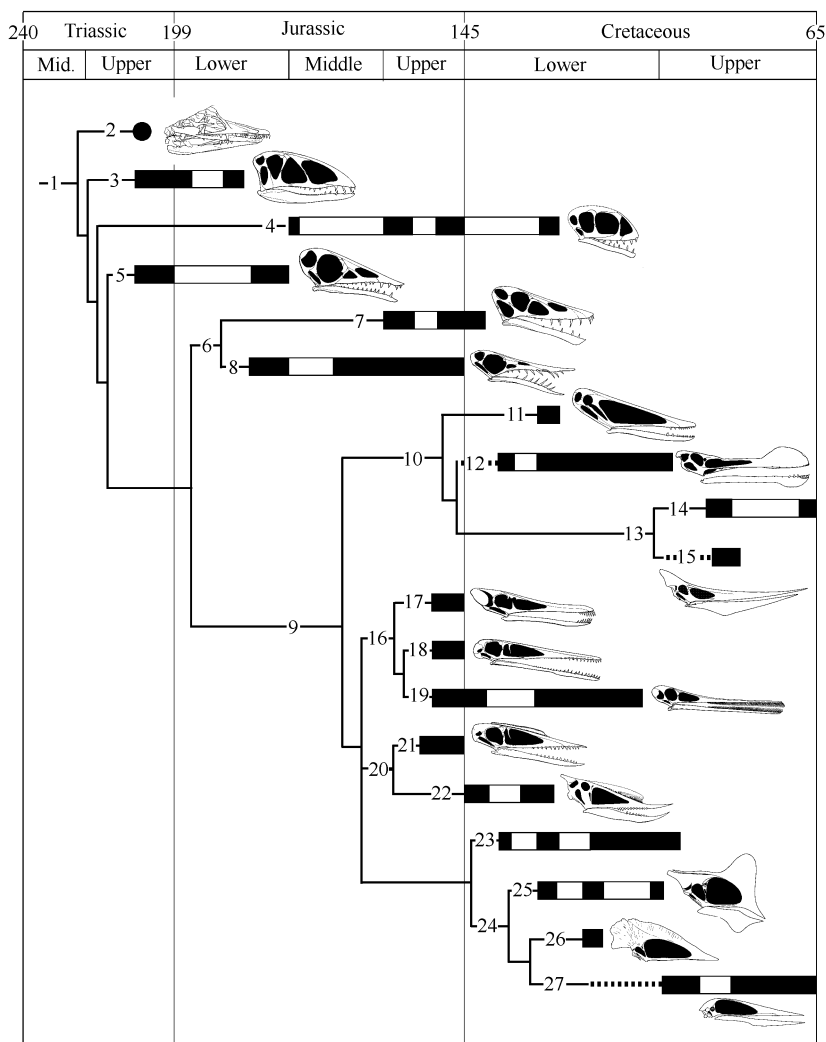


Fig. 2 The evolutionary history of pterosaurs based on the phylogeny of Unwin (2005) and stratigraphic records published up until mid 2005.

Known records for each clade are indicated by the solid region of each bar. Unfilled portions of bars indicate intervals during which the clade must have existed, but is not represented by fossils. The main clades are as follows: 1, Pterosauria; 2, *Preondactylus*; 3, Dimorphodontidae; 4, Anurognathidae; 5, Campylognathoididae; 6, Rhamphorhynchidae; 7, Scaphognathinae; 8, Rhamphorhynchinae; 9, Pterodactyloidea; 10, Ornithocheeroidea; 11, Istiodactylidae; 12, Ornithocheiridae; 13, Pteranodontia; 14, Nyctosauridae; 15, Pteranodontidae; 16, Ctenochasmatoidea; 17, *Cycnorhamphus*; 18, *Pterodactylus*; 19, Ctenochasmatoidea; 20, Dsungaripteroidea; 21, basal dsungaripteroids; 22, Dsungaripteridae; 23, Lonchodectidae; 24, Azhdarchoidea; 25, Tapejaridae; 26, tupuxuarids; 27, Azhdarchidae. Beginning from the base of the cladogram, the skulls are as follows: *Preondactylus*, *Dimorphodon*, *Anurognathus*, *Campylognathoides*, *Scaphognathus*, *Rhamphorhynchus*, *Istiodactylus*, *Ornithocheirus*, *Pteranodon*, *Cycnorhamphus*, *Pterodactylus*, *Ctenochasma*, *Germanodactylus*, *Dsungaripterus*, *Tapejara*, *Tupuxuara*, *Zhejiangopterus*.



Despite the recent and in some cases dramatic improvement in our knowledge of pterosaur biology and evolutionary history, some aspects of these animals remain poorly understood. Prominent among these is their reproductive biology. For the last two centuries virtually nothing was known of this subject and there was no direct evidence to answer key questions such as: Did pterosaurs lay eggs (oviparity) or produce live young (viviparity)? If they laid eggs did they incubate them in-nests, or were they buried? When the young hatched (or were born) were they looked after by the parents or entirely self-sufficient? Naturally, the absence of evidence led to much speculation and some general ideas: that pterosaurs were oviparous, brooded their eggs in nests and cared for their young (since it was generally assumed that they would have been unable to fly for weeks or months after birth/hatching) became widely established.

The recent discovery of eggs apparently belonging to three different species of pterosaurs (Chiappe *et al.*, 2004; Ji *et al.*, 2004; Wang and Zhou, 2004) represents a major breakthrough for our understanding of pterosaur reproductive biology. These finds do not, by any means, enable us to tackle all the questions posed above, or the many other issues that stem from these questions, but they do allow several important issues to be resolved and we address one of those here: were all pterosaurs oviparous?

As mentioned, previously it was widely believed that all pterosaurs were likely to have been oviparous (e. g. Wellnhofer, 1991), and the several finds reported on in 2004 certainly appear to confirm this (Unwin, 2005). Recently, however, there have been counterclaims that at least some and possibly all pterosaurs were viviparous (Peters, 2004a, 2004b). It is possible (although as we argue here, highly unlikely) that both reproductive modes, oviparity and viviparity, were present in pterosaurs, since this does occur in at least two other diapsid groups: lizards and snakes (Shine, 1985). In this paper we review the fossil record of pterosaur eggs and present several lines of evidence that, we argue, support the idea of universal oviparity in pterosaurs.

Abbreviations

Institutional – **BMNH**, Natural History Museum, London, United Kingdom; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **JZMP**, Jinzhou Museum of Paleontology, Jinzhou, China; **MHIN-UNSL-GEO**, Museo de Historia Natural de la Universidad Nacional de San Luis, San Luis, Argentina; **MMP** Museo Municipal de Ciencias Naturales ‘Galileo Scaglia’, Mar del Plata, Argentina.

Anatomical – **ch**, cheiropatagium; **cp**, cruropatagium; **cr**, coracoid; **cv**, cervical vertebrae; **d**, dentary; **dv**, dorsal vertebrae; **fe**, femur; **ga**, gastralia; **hu**, humerus; **il**, ilium; **m**, maxilla; **mc**, metacarpal; **mt**, metatarsals; **pm**, premaxilla; **pr**, propatagium; **pt**, pteroid; **pu**, pubis; **ra**, radius; **sc**, scapula; **sh**, shell; **sk**, skull; **sv**, sacral vertebrae; **t**, tooth; **ti**, tibia; **ul**, ulna; **wd**, wing-finger phalanx; **wm**, wing-metacarpal; **wp**, wing-phalanx.



THE FOSSIL RECORD OF PTEROSAUR EGGS

19th and 20th Century finds

Egg-like fossils that were later attributed to pterosaurs were first reported from the Great Oolite (Middle Jurassic: Bathonian), of Hare Bushes Quarry near Cirencester, England, by Buckman in 1860 (see Cox *et al.*, 1999 for further details). The finds (BMNH R1890 and BMNH R3194) consisted of at least eight ovate structures each measuring about 44 mm long by about 28 mm in width and rather haphazardly clustered together. Buckman (1860) recognised that the fossils were probably reptile eggs and assigned them the name *Oolithes bathonicae*.

Subsequently, Carruthers (1871) reported on similar fossils from the Stonesfield Slate (Middle Jurassic: Bathonian) at Stonesfield, in Oxfordshire, England. The exact number of finds, held in the collections at Oxford University Museum and the British Museum (now Natural History Museum), London, was not specified, but two examples were figured (Carruthers, 1871, pl. xix, figs 4-7, 10). Unlike the eggs of *Oolithes bathonicae* these eggs were smaller, about 19 mm in diameter and spheroidal and thus acquired the name *Oolithes sphaericus*.

Carruthers (1871) also figured a fossil from the Wealden (Lower Cretaceous) of Brixton, Isle of Wight, England, that was originally thought to be a fruit, but which was identified by Carruthers as a small egg, just under 10 mm in diameter, and given the name *Oolithes obtusatus*.

Buckman (1860) had already suggested that *Oolithes* were the fossilized remains of reptile eggs and Carruthers (1871) concurred with this view since the external ornament on the various 'eggs' seemed to be similar to that of the eggs of extant reptiles. Carruthers went further, however, and suggested that the eggs may belong to turtles, or, citing the view of Seeley (1870b), also mentioned that they might be pterosaur eggs, since numerous fragmentary remains of the large rhamphorhynchid *Rhamphocephalus* had also been found in the Great Oolite and Stonesfield Slate (reviewed in Unwin, 1996).

Later, analysis of the structure of the egg-shell of *Oolithes* by van Straelen (1928) appeared to confirm the general idea that the eggs were reptilian and this proposal was also accepted more recently (Carpenter and Alf, 1994; Carpenter *et al.*, 1994). The most recent study (Cox *et al.*, 1999) also supported this conjecture and reported that the shell structure, examined using a scanning electron microscope, was similar to that of Recent and Pliocene sea turtles. It seems likely, therefore, that these and other eggs reported from what appears to have been the same quarry (Cox *et al.*, 1999), and now identified as *Testudo flexoolithus* (Hirsch, 1996) are those of turtles and not pterosaurs.

In the 'Illustrated Encyclopedia of Pterosaurs' Wellnhofer (1991: 162) mentioned the discovery in 1989 of egg-shell fragments at a site in the Upper Cretaceous of Big Bend National Park, Texas, USA, from which remains of the smaller morph of *Quetzalcoatlus* had been recovered. As noted by Wellnhofer (1991), there was no evidence to directly associate the egg-shell with the



pterosaurs and, to date, no further details of this find have been published.

In volume one of 'The Fossils of Solnhofen', published in 1994, Frickhinger figured an example of *Pterodactylus* sp. that is cited as containing an egg-like structure. The fossil, listed as in the collection of Dr Kariopp of Regensburg, Germany, consists of a semi-complete skeleton of *Pterodactylus* with a skull length of about 80 mm, which corresponds closely to the median skull size for *Pterodactylus kochi* (Wellnhofer, 1970). The 'egg' is visible as a spheric, ghost-like object, about 13 mm in diameter, preserved in the anteroventral region of the torso, immediately behind the shoulder girdle, and thus located in the thorax. Both the current location of this structure and its size, apparently somewhat wider than the likely width of the pelvis between the left and right ischia, do not support its interpretation as an egg. However, since it is possible that there was postmortem displacement of objects within the torso and the exact dimensions of the pelvis and thus the maximum width of the oviduct are unclear, further assessment of this interesting find is warranted.

IVPP V13758

The first undoubted pterosaur egg, IVPP V13758, was reported in 2004 by Wang and Zhou. The specimen was found in the Jingangshan Beds, which lie in the upper part of the Yixian Formation at Jingangshan in western Liaoning, China. In addition to other pterosaurs these deposits have also yielded plants, conchostracans, insect larvae, ostracods, gastropods, the osteoglossomorph fish *Lycoptera* (Zhang and Jin, 2003), the cryptodiran turtle *Manchurochelys*, an archaic lizard, *Yabeinosaurus* (Evans and Wang, 2005), and birds, including an egg with embryo (Zhou and Zhang, 2004). The Jingangshan Beds are dated at about 121 million years old and thus of middle Early Cretaceous (Aptian) age (Gradstein *et al.*, 2004).

The fossil (Fig. 3) is exceptionally well preserved, consisting of an elliptic shell measuring 53 by 41 mm and containing a complete embryo with a surprisingly well ossified and for the most part what appears to have been a naturally articulated skeleton. The tightly packed position of the embryo (Fig. 4) closely matches that adopted by embryos in the eggs of extant tetrapods. The head is folded down upon the chest and the vertebral column is oriented approximately parallel to the long axis of the egg. Most of the principal joints of the forelimb are partially or fully flexed. Remarkably, adjacent wing-finger phalanges often lie almost at right angles to one another, so that the right wing-finger, for example, now subtends a complete circle. This is in sharp contrast to the condition in most well preserved, articulated pterosaur skeletons representing post-hatching individuals where the joints in the wing-finger are almost always fully extended. The hind limbs are also partially flexed and drawn up beneath the body. Fossilised remains of soft tissues, including traces of the integument and wing fibres (aktinofibrillae), have also been reported (Wang and Zhou, 2004).

The poorly ossified epiphyses, presence of a grainy texture upon the surface of long bones, incomplete ossification of vertebrae, carpals and pedal digits and the apparent absence of fusion between elements such as the scapula and coracoid are all predictable features of the embryo since

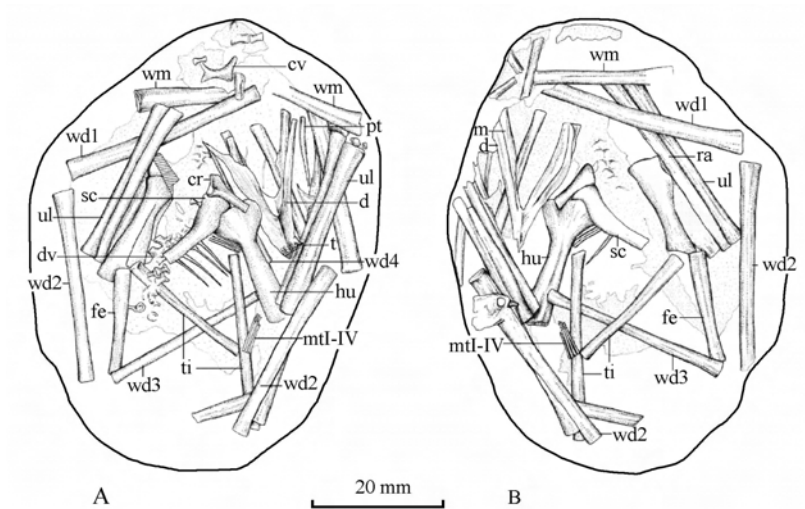


Fig. 3 IVPP V-13758, egg with embryo of an ornithocheirid pterosaur from the Lower Cretaceous Yixian Formation of Jingangshan region, Liaoning Province, China.
A, main specimen; B, counterpart. (Redrawn from Wang and Zhou, 2004).



Fig. 4 Reconstruction of the embryo and egg of IVPP 13758, based on an illustration published at www.dinosaur.net.cn.



they are also known in highly immature, but nevertheless older, post-hatching individuals of other pterosaurs (Wellnhofer, 1970; Bennett, 1996a; Codorniu and Chiappe, 2004). On the other hand, many elements of the skeleton including the pteroid, are at least partially ossified, suggesting that the embryo was near term and perhaps only a few days or even hours away from hatching.

Usually, embryos of amniotes can only be assigned to a broad taxonomic category, because features that might allow more precise identification generally only appear at more mature stages of development (Deeming and Unwin, 2004). In the case of IVPP V13758, however, morphological characters and morphometric data allow the identity of the embryo to be fairly precisely established. The presence of uniquely pterosaurian apomorphies such as a pteroid and hyper-elongate fourth (wing) finger (Wellnhofer, 1978; Sereno, 1991), confirm that the embryo is certainly a pterosaur, while the relatively elongate fourth (wing) metacarpal (only slightly shorter than the humerus) is an unambiguous apomorphy of Pterodactyloidea (Unwin, 2003a). Two proportions (Fig. 5) show that IVPP V13758 is an ornithocheiroid. First, the proportion of the metatarsal iii to the humerus is relatively low (less than 0.3), a ratio that is only found in ornithocheiroids and in-

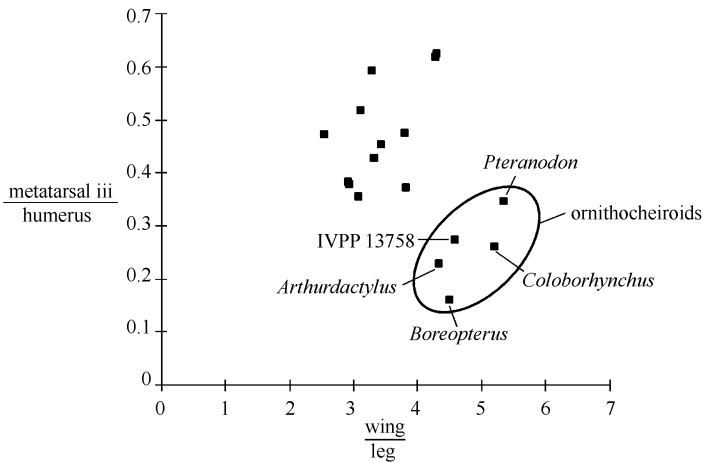


Fig. 5 Graph showing proportions of the wing to the leg plotted against proportions of the metatarsal iii to the humerus for IVPP 13758 and other pterodactyloids.

deed, at present, is restricted to ornithocheirids. In addition, the ratio of the fore-limb to hind limb is relatively high (greater than 4.5), a proportion that is almost exclusive to ornithocheiroids, although at least one other pterodactyloid, the ctenochasmatine *Pterodaustro* has a value of over 4.0. Plotted together (Fig. 5), data for these ratios demonstrate that ornithocheiroids, including IVPP V13758, form a cluster that is quite distinct from all other pterodactyloids. Moreover, IVPP V13758 is located closer to ornithocheirids than to pteranodontians such as *Pteranodon*, a relationship that is consistent with other ornithocheirid features of the embryo such as its relatively short wing-metacarpals.

Morphological characters support this conclusion. The warped deltopectoral crest (Fig. 3) is



quite unlike the relatively elongate forward-projecting crest of non-ornithocheiroids and is similar to that of ornithocheiroids, especially ornithocheirids such as *Coloborhynchus* (Kellner and Tomida, 2000). The presence of simple, slightly curved, sharp-pointed teeth in the anterior end of the mandible of IVPP V13758 closely resembles the dentition of ornithocheirids, but is different from that of other ornithocheiroids such as istiodactylids (blade-like teeth) and pteranodontians (toothless).

It seems highly likely that IVPP V13758 belongs to a species of ornithocheirid, two genera of which, *Haopterus* (Wang and Lü, 2001) and *Boreopterus* (Lü and Ji, 2005), have been reported from the Yixian Formation. Insofar as comparisons can be made, the proportions of IVPP V13758 more closely resemble those of *Haopterus* than *Boreopterus*. Moreover, some of the differences between *Haopterus* and IVPP V13758, such as the relatively short wing-metacarpal of the latter, can be accounted for by allometric growth trends already established for other pterodactyls (Codorniu and Chiappe, 2004). Further detailed studies are needed, however, to determine exactly how IVPP V13758 and *Haopterus* may be related.

JZMP-03-03-2

The middle Lower Cretaceous (Aptian) Jingangshan Beds of the Jingangshan area of Liaoning Province, China, have yielded a second pterosaur egg (Fig. 6), reported on by Ji *et al.* in 2004. This example is from the same locality and sequence as the first pterosaur egg from Liaoning, but according to Ji *et al.* belongs to a different taxon.

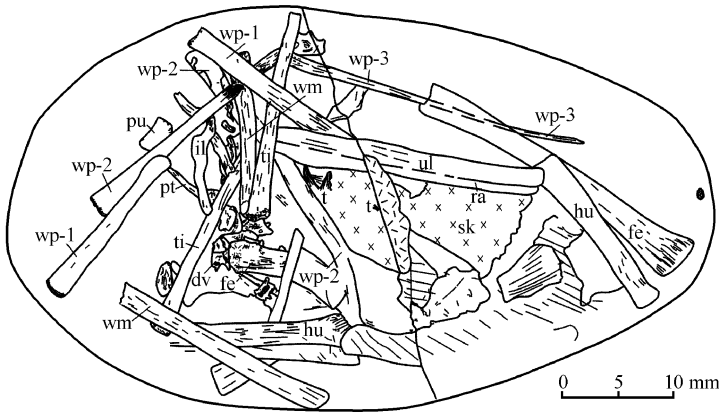


Fig. 6 JZMP-03-03-2, egg with embryo of a pterodactyl pterosaur from the Lower Cretaceous Yixian Formation of Jingangshan region, Liaoning Province, China. (Redrawn from Ji *et al.*, 2004).

The preservation of the egg is similar to that reported by Wang and Zhou (2004). The egg is complete, with remains of the shell, elements of the skeleton and evidence of soft tissues. It is surrounded by numerous fossilised insect larvae (*Ephemeropsis trisetalis*) and fish (*‘Lycoptera’ murroi*). The major dimensions of the egg are 63.7 mm by 36.4 mm indicating an egg that was longer and narrower than that described by Wang and Zhou. The shell is reported to be 0.25 mm thick.



The embryo appears to be less well articulated compared to that in IVPP V13758 and, although much of the skeleton seems to be visible, it is difficult to identify many elements with certainty. Small, curved, rather widely spaced teeth are clearly present and several fore limb elements including the humerus, radius/ulna and wing-finger phalanges can also be picked out, although details are generally not discernible. Parts of the pelvis and what may be the main elements of the hind limb are evident toward the broader end of the egg.

The presence of shallow, longitudinal grooves upon the shafts of the long bones and the rather poor ossification of many skeletal elements, especially the skull, vertebrae and pelvis, are consistent with the embryonic status of this individual. Compared with the IVPP V13758 embryo, JZMP-03-03-2 is less well ossified, perhaps indicating that in this case the embryo died and the egg was buried and fossilized at an earlier stage of development than in IVPP V13758.

The presence of what appears to be a pteroid and wing-finger phalanges demonstrate that JZMP-03-03-2 is pterosaurian, and the element identified as a wing-metacarpal is much more elongate than in any basal pterosaur, confirming Ji *et al.*'s determination of this embryo as that of a pterodactyloid. The presence of rather well-spaced, sharp-pointed teeth excludes the possibility that JZMP-03-03-2 is an azhdarchoid, all of which are toothless (Kellner, 2004), but leaves three alternatives.

Dsungaripteroid affinities seem unlikely, since Cretaceous forms have relatively stoutly built teeth (Young, 1973). On the other hand, the dentition of some ctenochasmatooids is rather similar and three genera, the cynorhamphid *Feilongus* (Wang *et al.*, 2005) and the ctenochasmatooids *Eosipterus* (Ji and Ji, 1997; Unwin *et al.*, 2000) and *Beipiaopterus* (Lü, 2003) have been reported from the Yixian Formation. Indeed, Ji *et al.* (2004) argued that features of JZMP-03-03-2 compared well with *Beipiaopterus* and, although they did not formally assign the embryo to this taxon, a close relationship was implied. The presence of just three phalanges in the wing-finger (Lü, 2003), rather than four, as in most pterosaurs, has not been satisfactorily demonstrated for *Beipiaopterus*, or for JZMP-03-03-2, and since this is the only feature that unites these two a close relationship between them has yet to be established. It should also be noted that according to Ji *et al.* (2004) there is an increase in length of wing-phalanges one to three, which is opposite to the pattern seen in *Beipiaopterus* and all other pterodactyloids, where the length of successive phalanges decreases. It may be that individual wing-phalanges of JZMP-03-03-2 have been mis-identified but, even so, this does not demonstrate a relationship between *Beipiaopterus* and JZMP-03-03-2.

A third alternative is that JZMP-03-03-2 is the embryo of a species of ornithocheirid, perhaps even the same species as IVPP V13758. Ji *et al.* (2004) reject this, but there is some evidence in favour of this idea. First, the dentition of JZMP-03-03-2 compares well with that of ornithocheirids such as *Haoipterus* (Wang and Lü, 2001). Secondly, the humerus has a rounded, seemingly warped deltopectoral crest, like that of other ornithocheiroids (see above) and that is, in some respects, rather similar to that of IVPP V13758. Thirdly, although the egg of JZMP-03-03-2 has a different shape to that of IVPP V13758, the estimated volume of each egg is remarkably similar,



51 cm³ in IVPP V13758 compared to 48 cm³ in JZMP-03-03-2 (egg volume = length x breadth² x kv, where kv corresponds to a correction factor of 0.57 [see Hoyt, 1979]), raising the possibility that the shape variation may reflect different compressional regimes rather than any real systematic difference. The apparently pliable nature of the egg-shell (Ji *et al.*, 2004) may have been an important contributory factor to this process.

In conclusion, we support the supposition by Ji *et al.* (2004) that JZMP-03-03-2 represents a pterodactyloid pterosaur, but argue that there is as much, or more, evidence in favour of ornithocheirid rather than ctenochasmatid affinities. Further study is needed in order to resolve the likely taxonomic relationships of this fossil.

MHIN-UNSL-GEO-V246

In the same edition of *Nature* that reported on the second pterosaur egg from China, there appeared a brief account of an embryonic pterosaur associated with fragments of egg shell, from the Lagarcito Formation at Loma del *Pterodaustro* in the north-western corner of San Luis Province in Argentina (Chiappe *et al.*, 2004). The beds at Loma del *Pterodaustro* are dated at about 100 million years BP, and thus Early Cretaceous (Albian) in age (Gradstein *et al.*, 2004). This sequence, thought to have accumulated in a large lake, has yielded a highly restricted vertebrate fauna consisting of fish and a single tetrapod, the ctenochasmatine pterosaur *Pterodaustro*, represented by several hundred individuals (Chiappe *et al.*, 1998, 2000).

The specimen, MHIN-UNSL-GEO-V246, consists of a complete skeleton preserved in a tightly packed pose (Fig. 7) that is remarkably similar to the pose of the embryo of IVPP V13758. The head is folded down upon the chest and the vertebral column lies sub-parallel to the long axis of the egg. The forelimbs are tightly flexed, the hands above the head and the wing-fingers curled around the body, and the legs are also fully flexed at the knee and ankle (Fig. 8). The main difference between MHIN-UNSL-GEO-V246 and IVPP V13758 is that the limbs of the former seem to be more tightly wrapped around the body, while in the latter they are more spread out. This probably reflects the much greater degree of broadening that the Chinese egg appears to have undergone, as it was compressed during compaction of the surrounding sediment, whereas the Argentinean specimen seems to have remained largely undistorted.

The porous texture of bone surfaces, poorly ossified ends of limb bones and lack of fusion between sacral vertebrae, or between the scapula and coracoid, are all consistent with an early stage of development (Bennett, 1993, 1995, 1996a; Codorniu and Chiappe, 2004; Chiappe *et al.*, 2004). The similarity in size and proportions to what appear to be newly hatched individuals of the same species of pterosaur (MHIN-UNSL-GEO-V241, MMP 1168, Codorniu and Chiappe, 2004) suggest that MHIN-UNSL-GEO-V246 was almost full term and probably near to hatching.

Only patches of the egg-shell are preserved, but these show a remarkably thin carbonatic layer only 0.03 mm thick and consisting of a single layer of calcite with crystals forming V-shaped eggshell units (Chiappe *et al.*, 2004). Originally, the egg appears to have been about 60 mm in length by 22 mm in breadth, and thus was of similar length to the second Chinese specimen, but

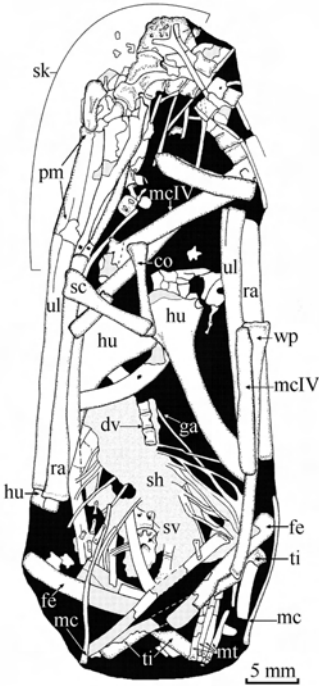


Fig. 7 MHIN-UNSL-GEOV 246, embryo associated with patches of egg shell of the ctenochasmatine pterosaur *Pterodaustro guinazui* from the Early Cretaceous Lagarcito Formation of Loma del *Pterodaustro*, San Luis Province, Argentina.

(Redrawn from Chiappe *et al.*, 2004).



Fig. 8 Restoration of MHIN-UNSL-GEOV 246, reproduced with permission from L. Chiappe and the Natural History Museum of Los Angeles County, USA.

much narrower and with an estimated volume (17 cm^3) that is only about one third that of the Chinese eggs. This is a little surprising because, in terms of its major dimensions, the embryo of MHIN-UNSL-GEO-V246 with a wingspan of 270 mm and a leg length of about 45 mm (based on MHIN-UNSL-GEO-V 241) is slightly larger than the embryo of IVPP V13758, which has an estimated wingspan of about 250 mm and a leg length of 30 mm.

That MHIN-UNSL-GEO-V246 is pterosaurian is demonstrated by the presence of remarkably long fore-limbs, an elongate and robust wing-metacarpal and a remarkably elongate digital phalanx, identified as phalanx one of the wing-finger. A relatively elongate wing-metacarpal (85% the length of the humerus) and the apparent absence of a well-developed fifth toe indicate that this individual is a pterodactyloid (Kellner, 2003; Unwin, 2003a). The comparative lengths of limb elements, in particular the relatively long metatarsal iii compared to the tibia and the relatively short ulna compared, for example, to the femur, are very similar to the corresponding proportions in *Pterodaustro guinazui* (Fig. 9). Moreover, the proportions of other limb elements also show a good correspondence with this taxon and correspond very closely to the bone lengths for two neonatal individuals from the same site that have also been assigned to *Pterodaustro guinazui* (Codorniu and

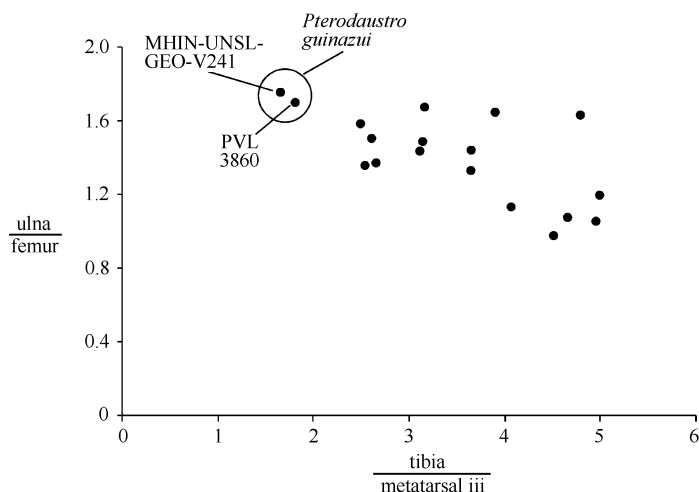


Fig. 9 Graph showing the proportions of the tibia to the metatarsal iii plotted against the proportion of the ulna to the femur for a selection of pterodactyloid pterosaurs including ctenochasmatooids, dsungaripteroids, azhdarchooids and ornithocheiroids. MHIN-UNSL-GEO-V 241 is used here as a proxy for MHIN-UNSL-GEO-V 246 since all measurable elements of the latter (humerus, ulna, wing-metacarpal, wing-finger phalanx one, femur) are between 0.95 and 1.01 times the size of the corresponding element of the former .
(see also Chiappe *et al.*, 2004).

Chiappe, 2004). This conclusion is strongly supported by the presence of a highly elongate rostral part of the skull, an apomorphy of ctenochasmatid pterosaurs (Unwin, 2002, 2003) and the observation that only a single species of pterosaur has been found at the Loma del *Pterodaustro* (Chiappe *et al.*, 1998, 2000).

DISCUSSION

Pterosaur Ingroup Relationships and Their Implications for the Distribution of Oviparity

By adopting an assumption of parsimony and mapping the occurrence of taxa known to have been egg-bearing onto the cladogram shown in Fig. 10 we can infer the minimum limits of a clade whose members are likely to have been oviparous. That clade corresponds to the Pterodactyloidea. This is because the first pterosaur egg to be described, IVPP V13758, appears to have belonged to a species of ornithocheirid pterosaur, a member of Ornithocheiroidea, while MHIN-UNSL-GEO-V246 is ascribed to *Pterodaustro* which is a ctenochasmatine and thus included within Ctenochasmatoidea. The most recent common ancestor of these two clades is also the most recent common ancestor for Pterodactyloidea, irrespective of how Ctenochasmatoidea, Dsungaripteroidea and Azhdarchoidea are related to one another, because Ornithocheiroidea almost certainly lies outside the

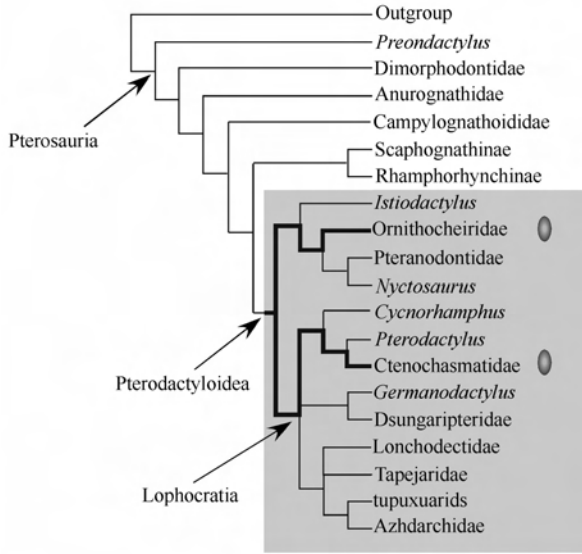


Fig. 10 Distribution of eggs within Pterosauria. The phylogeny is based on Unwin (2003a), but with some changes: Lonchodectidae is located in a sister group relationship with other azhdarchoids (see Unwin, 2005), Tapejaridae is restricted to *Sinopterus*, *Huaxiapterus* and *Tapejara* (see Lü *et al.*, 2006) and tupuxuarids include *Tupuxuara* and *Thalassodromeus*. The thick line indicates the most recent common ancestor of known egg-bearing taxa, while the grey box encloses all descendants of this common ancestor.

clade Lophocratia, to which the former three belong (Unwin, 2003a).

Although the topology of analyses by Kellner (2003, 2004; see also Wang *et al.*, 2005) differ somewhat from that shown in Fig. 10, mapping the known distribution of oviparous pterosaur taxa onto these cladograms yields the same result: a most parsimonious assumption that all members of the Pterodactyloidea laid eggs. Ingroup relationships do not permit further inferences regarding the distribution of oviparity, or viviparity within pterosaurs, but some insights can be gained by considering the relationship of pterosaurs to other diapsids.

Relationships of Amniota and Their Implications for Pterosaur Oviparity

The relationships of major amniote clades are now fairly well understood and since several of these clades are still extant it is possible to use data on these and several extinct clades in which eggs or embryos are preserved within the mother (see Deeming and Unwin, 2004), to establish general patterns of distribution of oviparity and viviparity within Amniota (Fig. 11). By adding the clade Pterosauria to this cladogram it should be possible to infer whether pterosaur ancestors are likely to have been oviparous or viviparous.

However, the strength of this approach is weakened by two problems. First, the reproductive mode of many extinct groups is still unknown, consequently the exact distribution of oviparity and viviparity has yet to be established. Secondly, and more seriously, the relationships of pterosaurs to other diapsids is far from clear. At present there are at least four different competing hypotheses, in

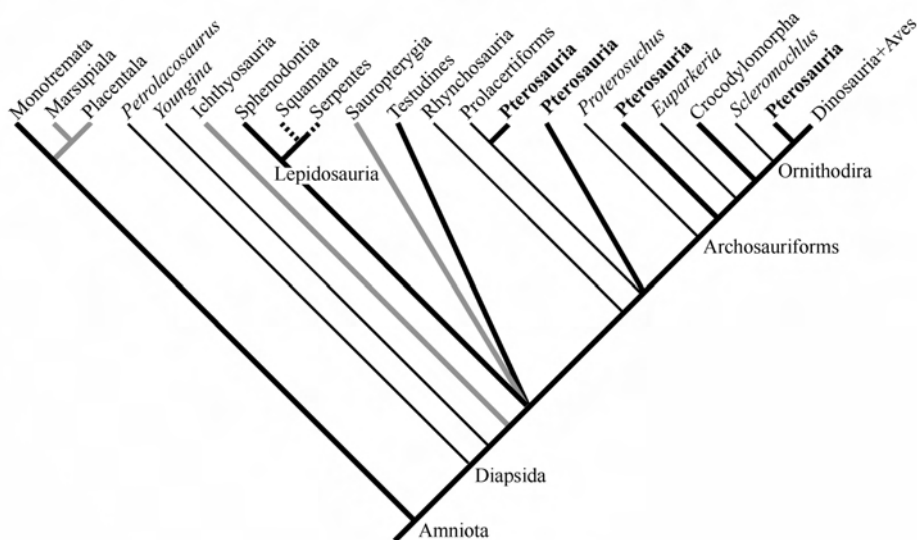


Fig. 11 The distribution of oviparity and viviparity in amniotes. Cladogram based on Benton (2004). Taxa that are known to have been oviparous are shown with a thick black line, taxa that are wholly viviparous are indicated by a grey line and taxa in which most clades are oviparous, but several are partially or fully viviparous are indicated by a dashed line. Extinct taxa in which the condition of oviparity or viviparity is as yet unknown are indicated by a thin black line. Currently, there are four hypotheses as to the relationships of Pterosauria to other amniotes: **A**, as a sister, or near sister group to Dinosauria + Aves (e.g. Gauthier, 1986; Sereno, 1991; Benton, 1999); **B**, as basal archosaurs (Wellnhofer, 1978; Bennett, 1996b); **C**, in an unresolved trichotomy with Prolacertiforms and Archosauriforms (Unwin, 2005); **D**, as a member of Prolacertiforms in a sister group relationship with *Shanvopteryx* (e.g. Peters, 2000). The implications of this cladogram are that oviparity is plesiomorphic for amniotes and that the assumption of universal oviparity in pterosaurs is more consistent with the known distribution of reproductive modes in amniotes than an assumption that basal pterosaurs, at least, were viviparous.

which pterosaurs are variously considered to be ornithodirans (Gauthier, 1986; Sereno, 1991; Benton, 1999), basal archosaurs (Bennett, 1996b), a sister taxon to certain prolacertiforms (Peters, 2000), or in an unresolved relationship with prolacertiforms and archosauriforms (Unwin, 2005).

If pterosaurs are ornithodirans then it seems highly likely that the plesiomorphic condition for the group was oviparity since this mode of reproduction is universal in the two extant groups (crocodiles and birds) that bracket ornithodirans (Thompson and Speake, 2004). If pterosaurs lie outside Ornithodira, then oviparity is still the most likely reproductive mode for ancestral forms (Fig. 10), but the demonstrated presence of viviparity in Ichthyosauria and Sauropterygia weakens this inference since, although less likely, it is possible that prolacertiforms or even basal archosaurs were also viviparous. We are inclined to reject the latter idea, however, since viviparity in Mesozoic marine reptiles seems to be directly related to their aquatic life style, and this certainly does not



apply to basal archosaurs, or most prolacertiforms.

Taphonomic Evidence for Oviparity in Pterosaurs

Another potential method of assessing likely reproductive modes in pterosaurs concerns the evidence, or rather absence of evidence, for oviparity. Several groups of extinct diapsids (mosasaurs, ichthyosaurs and plesiosaurs) and at least one mammal, the Messel horse *Propalaeotherium* (Franzen, 1992), are known to have been viviparous because fossilized remains of one or more embryos have been found preserved within the mother (see Deeming and Unwin, 2004, for further details and references). If some pterosaurs were viviparous we might expect to find evidence for this in species represented by complete, or largely complete, well preserved skeletons, especially in those cases where large numbers of individuals have been collected. Such evidence has not yet been found in any pterosaur.

Several well-preserved individuals (mainly *Eudimorphodon*) are known from the Upper Triassic of northern Italy and Austria (Dalla Vecchia, 2003), and several dozen examples of *Dorygnathus* and *Campylognathoides* have been reported from the Holzmaden Shales of southern Germany (Wellnhofer, 1991), a sequence that has also yielded many pregnant ichthyosaurs (Böttcher, 1990; Deeming *et al.*, 1993). Many of these finds of pterosaurs are adult individuals, but not one is associated with remains that might be interpreted as embryos. The same is true for the Late Jurassic Solnhofen Limestones of southern Germany, which have yielded over a thousand individuals, including several hundred examples of *Rhamphorhynchus muensteri*, many of which appear to have been mature at the time of death (Wellnhofer, 1975; Bennett, 1995). The Jehol Group of north-east China has also yielded over one hundred individuals belonging to a wide variety of pterosaurs (Wang *et al.*, 2005), many of them exceptionally well preserved, but the only evidence of embryos so far has been found in pterosaur eggs. At least two thousand individuals of *Pteranodon* have been recovered from the Late Cretaceous Niobrara Chalk (Bennett, 2001; Everhart 2005), but not one of these has been reported in association with the remains of smaller individuals.

Additional well-preserved pterosaur remains are also known from other deposits (see Wellnhofer, 1991; Unwin, 2005, fig. 3.9). Again, mature individuals are common among these finds but, as elsewhere, there is no evidence for embryos either within or even associated with a potential parent. Examining the issue from a different view point, it can be shown that almost all the major pterosaur clades identified in Fig. 10 are represented by at least several (and occasionally many) relatively well preserved mature individuals, not one of which has yielded any evidence of association with small and potentially embryonic remains.

Admittedly, ‘absence of evidence is not evidence of absence’, which means that the taphonomic test for reproductive modes is not especially powerful. That said, at present, there is still no direct fossil evidence for viviparity in any pterosaur.

Why Are Pterosaur Eggs So Rare?

It may seem surprising that direct evidence for oviparity in pterosaurs has only recently been



discovered, in that eggs of contemporaneous groups such as dinosaurs have been known for more than a century and are represented by tens of thousands of remains (e. g. Carpenter *et al.*, 1994; Mikhailov, 1997). An important feature of the newly discovered pterosaur eggs provides a simple explanation for this pattern. Dinosaur egg-shells and those of their descendants, the birds, are relatively heavily calcified, as are those of crocodilians and some turtles which have rigid shelled eggs (Thompson and Speake, 2004). Some turtles have less heavily calcified, pliable egg shells, while parchment-like egg shells typical of most squamates and sphenodontians are least heavily calcified and may even lack a continuous calcareous layer (Thompson and Speake, 2004). A simple prediction that can be made from these observations is that dinosaur eggs are likely to have the best fossil record, followed by birds, crocodiles and turtles, while sphenodontians and squamates are likely to have the worst record. Recent reviews of the fossil record of amniote eggs (Hirsch, 1994; Mikhailov, 1997) bear out this prediction.

According to Chiappe *et al.* (2004), the *Pterodaustro* egg has a calcareous layer that was only 0.03 mm in thickness, while Ji *et al.*, (2004) argued that the shell of JZMP-03-03-2 was not calcified, and the same seems to be the case for IVPP V13758. This renders it likely that pterosaur eggs had a pliable, or possibly even parchment-like shell and, as a consequence, a relatively low preservation potential. This explains why pterosaur eggs have, so far only been found in circumstances where exceptional preservation is possible and why they are likely to continue to remain extremely rare.

An Alternative View?

Even before the discovery of pterosaur eggs it was widely assumed that all pterosaurs were oviparous (e. g., Wellnhofer, 1978, 1991), and this assumption can now be regarded as almost universal. An alternative, and dissenting, view has been expressed by Peters (2004a, 2004b, 2005). He has suggested that the egg and embryo reported on by Wang and Zhou (2004) can be better interpreted as the remains of a tiny adult pterosaur that fed on eggs and, having crawled inside the shell of an egg belonging to some other unspecified tetrapod, died and was subsequently preserved there. In addition, Peters (2004a, 2005) claims to have discovered fossilised remains of embryos and babies preserved either within, or adjacent to, individuals of several pterosaurs including *Dendrorhynchoides*, *Pterodactylus*, *Haopterus* and *Zhejiangopterus*.

Addressing the interpretation of Wang and Zhou's egg and embryo first, several observations speak against Peters' interpretation. As noted above, the embryo exhibits many features indicative of osteological immaturity, among which, as Bennett (2005) has noted, the ends of long bones are very simple shapes, suggesting this individual was more immature than any previously known pterosaur. Moreover, the position of the embryo corresponds closely to the typical pose adopted by embryos in eggs of other tetrapods. It is not at all clear (and no reason has been advanced) why an adult pterosaur should adopt such a pose. Moreover, it is extremely doubtful that, even should it have chosen to have done so, it could accomplish this pose because it would have required extreme flexion, almost into a complete circle, of the wing-finger, which is widely regarded as having been



a stiff, rod-like structure in post-hatching individuals (e. g., Wellnhofer, 1991; Bennett, 2001). Furthermore, apart from the extreme unlikelihood of the taphonomic scenario proposed by Peters, his interpretation can also be firmly rejected on the grounds that such tight packing of an individual within an egg-shell is only possible if it has developed within the egg.

The issue of the embryos or babies associated with their mothers forms only part of a larger spectrum of claims made by Peters (2004a, 2004b, 2005) regarding pterosaur anatomy and based on a technique that involves enhancement and interpretation of digital images. By manipulating images, in many cases captured from printed material such as books and papers, or the internet, and thus of relatively low quality, Peters claims to be able to use computer software such as ‘Photoshop’ (Knoll *et al.*, 2003) as a digital microscope. Attempts to replicate this technique (Bennett, 2005) failed to corroborate any evidence of the embryos, babies, or many other features that Peters claims to have found in pterosaurs and other groups of fossil reptiles. Furthermore, examination of specimens using microscopes and employing both natural and ultra-violet light, in which embryos and babies have been reported by Peters to be present, failed to discover any evidence to support these claims (see, for example, Bennett, 2005: fig. 6). In one notorious case Peters reconstructed an extremely large frill associated with the crest of *Nyctosaurus* (Bennett, 2003) and added another frill that extended along the dorsal midline of the body from the base of the skull to the base of the tail (illustrated in Bennett, 2005) – apparently unaware that the chalk slab that supposedly bore evidence of these structures had been scraped clean during preparation and covered with white paint (Bennett, 2003). Consequently, it would seem that what Peters has reported are merely details of the surface topography of the sediment surrounding fossils, further modified, in many cases, by preparation. We concur with Bennett (2005) that the structures identified by Peters are purely artefacts stemming from the technique employed, thus any conjectures based on these claims can be safely ignored.

CONCLUSIONS

It seems unlikely that it will ever be possible to demonstrate, on the basis of fossil finds, that all species (or at least all known species), of pterosaur were oviparous. That said, the available evidence in favour of this assumption is highly persuasive. The undoubted presence of oviparity in ctenochasmatoids and ornithocheiroids renders it highly likely that all pterodactyloids, at least, were oviparous. Moreover, irrespective of the exact relationship of pterosaurs to other diapsids, the widespread distribution of oviparity in this clade suggests that the ancestors of pterosaurs were also oviparous, as were all their descendants, including basal pterosaurs and pterodactyloids.

This conclusion is further supported by the observation that reproductive systems tend to be conservative. In the other two groups of true flying vertebrates, birds and bats, the reproductive mode, oviparity and viviparity respectively, is invariable, and the same principle is also true of most extant clades of tetrapods (the major exception being squamates). Since at least two and probably three different species of pterosaurs are certainly known to have been oviparous it is most



parsimonious to assume that this was generally true for these animals. Finally, the presumption of universal oviparity in pterosaurs is also consistent with the complete lack of evidence, in any pterosaur, of an embryo preserved within or adjacent to the parent.

ACKNOWLEDGMENTS

We thank Elke Siebert for producing Fig. 4. Chris Bennett kindly provided several hard to obtain PDF's and Wang Xiaolin, Zhou Zhonghe and Luis Chiappe generously provided materials for Fig. 3, 7 and 8. Johannes Mueller advised on (but does not necessarily agree with all) the relationships shown in Fig. 11. David Unwin thanks the Institut für Paläontologie, Museum für Naturkunde, Humboldt Universität zu Berlin for logistical support. We are very grateful to Eric Buffetaut and Luis Chiappe for their comments on earlier versions of the MS and to Louis Jacobs for his editorial assistance.

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所有翼龙都是卵生的吗

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摘要 最近对中生代飞行爬行动物——翼龙方面的研究已经取得了许多进展,而且对于翼龙的古生物学、系统发育关系及进化史的一些基本问题的认识现在已取得一致意见。翼龙生殖生物学研究已通过三枚鸟掌龙代表不同翼龙含胚胎的开始。两枚发现于中国下白垩统义县组,属于翼手龙类,而且一枚根据其独特的肢骨比例(比如相对短的第Ⅲ指骨及相对长的前肢)和一些包括凸缘状的肱骨三角嵴等形态特点可以明确地归入鸟掌龙科。第三枚来自阿根廷 Loma del 早白垩世的南方翼龙(*Pterodaustro*)可以非常接近地与该地点唯一已知、刚孵化及与 *Pterodaustro guinazui* 个体相比,从而可以确定,它毫无疑问地属于该种。一些证据支持卵生在翼龙类中是普遍存在的观点:① 梳颌翼龙类和鸟掌龙类的卵生现象作为最小推论,显示了至少所有翼手龙类是卵生的;② 卵生在双孔类广泛分布并且不论翼龙类在这一进化枝的确切位置如何(当前争论激烈的问题),尤其是如果翼龙类证明是 ornithomimids,那么翼龙类祖先是卵生生殖方式而不是胎生;③ 到目前为止,在翼龙类中完全缺少任何胎生的证据。可能是翼龙钙化程度很弱或者甚至为无钙化的软壳或壳为羊皮纸一样的了。这或许是因为与其它类群,例如具有钙化好的硬壳的恐龙和鸟相比,翼龙非常稀少的主要原因。